EVIDENCE OF SALINITY-INDUCED ECOPHENIC VARIATION IN CORDGRASS (SPARTINA FOLIOSA TRIN.)

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ABSTRACT

Results of culturing two height forms of *Spartina foliosa* in NaCl-treated nutrient solutions indicate that they are ecophenes. Growth was best in moderately saline solution and inhibited in fresh water and in a 1.2 osmolal (35 ppt) solution. Comparison of these results with soil salinity from areas supporting populations of each form suggest that the height of *S. foliosa* is influenced by local soil salinity conditions.

Spartina foliosa Trin. is a dominant plant species of the lower and mid-littoral zones of California salt marshes (Macdonald and Barbour 1974). The lower limit of its distribution is thought to be controlled by tidal inundation (Hinde 1954, Rowntree 1973). Its upper limit of distribution, which generally coincides with the mean high water (MHW) level, is governed by high soil salinity (Mahall and Park 1976b). Height and biomass of plants growing in this area of the marsh are generally less than in plants growing at lower intertidal elevations (Purer 1942, Atwater and Hedel 1976, Mahall and Park 1976a).

A population of *S. foliosa* in which adults grow only to 20–30 cm in height occurs along the eastern shoreline of San Francisco Bay. This marsh, located at the mouth of the Alameda River, is situated relatively high in the intertidal zone and is probably a remnant of a more extensive, pre-existing marsh (Mason 1976).

The difference in height between plants growing at high and low intertidal areas has led to the recognition of two forms of *S. foliosa* (Anonymous, 1976). The "robust" form is stout culmed, 0.3–1.2 m tall, and inhabits the lower littoral zone. The "dwarf" form is 0.2–0.3 m tall and typically occurs in the mid-littoral zone. The height distinction between the forms was adopted from criteria established for height forms of *Spartina alterniflora* (Adams 1963, Cooper 1974), a closely related species (Mobberley 1956) that occurs as the dominant vascular plant species of the lower and mid-littoral zones of East and Gulf Coast salt marshes.

The existence of height forms of *Spartina* sp., each occupying rather

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distinct elevational zones within the marsh, has generated studies to determine if the forms are ecotypes, and thus genetically distinct, or ecophenes, and thus genetically homogeneous. Parnell (1976) determined that $2n = 60$ for both the robust and dwarf forms of *S. foliosa*. Based upon chromosome number, then, there is no evidence that these two forms are different polyploid races. However, the same chromosome number for both forms does not negate the existence of ecotypes (Clausen et al. 1941). Based upon results of a field transplant experiment from which data were collected for more than a year, Harvey (1976) concluded that the forms were ecophenes and the variation in height was a physiological response to environmental gradients associated with tidal elevation.

With the exception of elevation, no environmental factors were measured in the study by Harvey (1976), and it is therefore not possible to correlate morphological variation with any specific environmental gradient(s) that may exist as a function of tidal elevation.

It is well documented that soil salinity is a major factor influencing growth and plant distribution within salt marshes (Chapman 1938, 1939; Mall 1969, Mahall and Park 1976b, Penfound and Hathaway 1938, Purer 1942). Furthermore, Mooring et al. (1971) and Nestler (1977) have shown that height of *S. alterniflora* is inversely related to salinity, suggesting that the height forms of this species are ecophenes.

In this study, the genecologic relationship of dwarf and robust *S. foliosa* was further investigated by examining the relative effect of salinity on these height forms under controlled laboratory conditions. It was hypothesized that the height forms are ecophenes and that the morphological dissimilarity observed in the field would vanish when both forms were exposed to a uniform, controlled environment. In order to relate morphological responses to actual field conditions, an assessment was made of the level of soil salinity each form was exposed to during a growing season.

Methods

Soil samples and plants were collected from two marshes. Palo Alto marsh is located on the western shore of San Francisco Bay at approximately 37°27′N, 122°06′W. *Spartina foliosa* and *Salicornia virginica* L. are co-dominant. Robust *S. foliosa* (1–1.5 m tall) is found in monospecific stands at the low intertidal elevations and along creek channels. There appears to be a clinal variation in height associated with intertidal elevation because at the *Spartina–Salicornia* ecotone (roughly MHW), *S. foliosa* is typically 20–50 cm tall.

Alameda Creek marsh (37°36′N, 122°07′W) is located on the eastern shore of San Francisco Bay at the mouth of Alameda Creek. The marsh is dominated by *Salicornia virginica* and dwarf *Spartina foliosa* (adult plants are 20–30 cm tall). *Spartina* occurs most extensively as

a monospecific stand along the shoreward 10 m of the marsh. It is also found hugging the edges of shallow tidal creeks that traverse the marsh.

Soil samples were taken in 1977 at the beginning (May) and end (October) of the growing season from three 3 × 6 m plots staked out in each marsh. The plots were placed so that discrete samples could be taken along the portion of the intertidal zone inhabited by *S. foliosa*. At Palo Alto, plot 1 (PA 1) was located within a stand of robust plants at the lower limit of intertidal distribution of *S. foliosa*. Plot 2 (PA 2) was located adjacent to a tidal creek within a stand of robust *S. foliosa*. This area was higher in the intertidal zone than plot 1. Plot 3 (PA 3), the highest intertidal area sampled, was located at the *Spartina–Salicornia* ecotone. At Alameda Creek, the sample plots were located along a transect that ran the width of the marsh. Plot 1 (AC 1) was located within the strip of *S. foliosa* that occupied the shoreward 10 m of the marsh. Plot 2 (AC 2) was at the *Spartina–Salicornia* ecotone, roughly 4 m from plot 1. Plot 3 (AC 3) was located within a small stand of *S. foliosa* that was restricted to the edges of a salt pan and an adjoining tidal creek. This pan was in the high marsh, an area dominated by *Salicornia*.

Soil samples were collected with a stainless steel soil corer with a 2 cm inner diameter. The cores were immediately sectioned horizontally into 0–5 cm, 5–15 cm, and 15–25 cm soil layers and the sections were sealed separately in plastic bags. The salinity of the root zone was calculated as the mean salinity of the 5–15 cm and the 15–25 cm soil layers. The determination of soil salinity was modified from Mahall and Park (1976b): water-soluble salts were extracted from a soil sample that had been dried at 100°C, and the osmolality of the extract was measured on a Wescor-model 5100 vapor pressure osmometer. Salinity of the original soil solution was calculated as osmole kg^{-1} H_2O.

Dwarf plants were collected from Alameda Creek on 17 March 1978, and robust plants were collected from Palo Alto on 22 March 1978. At Alameda Creek, all the plants were collected along the shoreward edge of the marsh where plot 1 was located. Plants from Palo Alto were collected from the areas where plots 1 and 2 were located. Alameda Creek was selected as the sole source of dwarf plant material. If the forms are ecotypes, then the robust form appears to be completely selected against at Alameda Creek. Thus, this population may represent a relatively homogeneous genetic stock of dwarf individuals. If both the dwarf, i.e., plants at the *Spartina–Salicornia* ecotone, and the robust form were collected from Palo Alto marsh, the expression of genetic differences between them may be diminished due to the greater potential for gene flow between sympatric forms. In order to collect young dwarf and robust plants of roughly the same age, plants approximately the same height with two expanded leaves were preferentially selected from both marshes.

All the plants collected for this study appeared to be new shoots sprouting from underground rhizomes, the species' primary means of reproduction. Asexual reproduction assures that the collected plants were representative of the respective forms observed at each marsh. The parents could not be determined, thus the samples were randomized with respect to the intrinsic genotypic variation within each population.

The plants were carefully uprooted so as to leave soil around the roots. Soil was later rinsed from the roots with tapwater in the laboratory. The plants were immediately rooted in vermiculite, and kept in a greenhouse until May, by which time they had fully recovered from transplanting (a well-developed root system was established, and the shoots had begun to grow).

On 12 May 1980, plants of each form were distributed evenly among four tubs, each containing 20 l of full strength nutrient solution (Machlis and Torrey 1956). Because *Spartina* sp. may require high levels of iron for successful growth (Adams 1963), the concentration of iron (as FeEDTA) was increased from 5 ppm to 10 ppm. Each solution was mixed and aerated by bubbling air through two plastic air diffusers. The air was supplied at a uniform rate by a filtered manifold system. Concentrations of 0.4 osmole kg^{-1} H_2O (11.7 ppt), 0.8 osmole kg^{-1} H_2O (23.4 ppt), and 1.2 osmole kg^{-1} H_2O (35.1 ppt) were established in three tubs by adding reagent grade NaCl at a rate of 0.2 osmole kg^{-1} H_2O every five days (Mahall and Park 1976b). Results of the field soil sampling were used to set the upper limit of the salinity range. The remaining solution consisted of nutrient solution only and served as a control against which salinity effects could be compared. The measured osmolality of this solution was 0.054 osmolal. The salinity of the solutions was monitored, and distilled water and/or NaCl were added as needed to maintain the proper concentrations. Nutrients were added at half strength every four weeks to supplement losses. The mean pH values for the control and the 0.4, 0.8, and 1.2 osmolal treatments were 6.3, 6.8, 7.0, and 6.7, respectively. Ambient air temperatures were maintained at 26°C, and relative humidity at 50%.

At the beginning of the experiment, 19 dwarf and 20 robust plants were measured for height, dry weight, leaf area, and leaf weight ratio (g leaves/g whole plant). Height was measured from the first visible node on the culm directly above the roots to the tip of the longest leaf. Leaf area was determined by treating each leaf as an isosceles triangle (Nestler 1977). Leaf weight ratio was calculated from the dry weight. The material was dried at 80°C for at least 24 hours in a forced draft oven. Plants in the culture solutions were harvested after 12 weeks.

One-way and two-way analysis of variance was used for statistical analysis of the data. Data for leaf area and leaf weight ratio were normalized by square root and arcsine transformation, respectively (Sokal and Rohlf 1969). In cases where the variances of the samples

TABLE 1. HEIGHT, DRY WEIGHT, LEAF AREA, AND LEAF WEIGHT RATIO OF DWARF AND ROBUST FORMS OF *Spartina foliosa* PRIOR TO TREATMENT IN CULTURE SOLUTION.

	Dwarf (n = 19)	Robust (n = 20)
Height, cm ($\bar{x} \pm$ S.E.)	24.7 ± 2.4	23.6 ± 1.1
Dry wt., g ($\bar{x} \pm$ S.E.)	0.307 ± 0.068	0.369 ± 0.039
cm^2 $leaf^{-1}$ ($\bar{x}$; 95% C.L.)	2.99; 2.53–3.50	3.99; 2.89–3.96
Leaf wt. ratio ($\bar{x}$; 95% C.L.)	0.239; 0.198–0.283	0.152; 0.132–0.172

being compared were not homogeneous, the Mann-Whitney test was used (Sokal and Rohlf 1969). Differences were considered significant when $\alpha < 0.05$.

RESULTS

Height, dry weight, and individual leaf area were not significantly different ($p > 0.05$) between the robust and the dwarf form when the culture experiment was started (Table 1). The leaf weight ratio of the dwarf form was significantly higher ($p < 0.001$) than that of the robust form. This difference was partially attributed to the heavier culm characteristic of the robust form. Additionally, the robust plants had a more extensive root and rhizome system, decreasing the dry weight of the leaves relative to the whole plant.

Survival of the two forms was similar after 12 weeks exposure to the same salinity (Table 2). Although the concentration of Fe was increased to 10 ppm, symptoms of Fe deficiency began to appear after about 45 days. Chlorosis was exhibited by all plants, but it was most pronounced in the plants in freshwater and the 0.4 osmolal treatment. Iron deficiency symptoms have also been described for cultured adult and seedling *S. alterniflora* (Adams 1963, Mooring et al. 1971). At present, it is not known if these observations are the result of a physico-chemical interaction between Fe and NaCl (Adams 1963), whereby

TABLE 2. SURVIVAL OF DWARF AND ROBUST FORMS OF *Spartina foliosa* GROWN IN SALINE CULTURE SOLUTION.

	Number of surviving plants	
Treatment	Dwarf	Robust
Control	10	7
0.4 osmolal	8	9
0.8 osmolal	17	16
1.2 osmolal	12	12

Fe availability to the plant is enhanced at high ionic strengths, or if there is a physiological requirement for one or both NaCl ions (Mooring et al. 1971). Mooring et al. (1971) reported that chlorosis was relieved by foliar application of ferrous sulfate; however, in our study, foliar spraying of FeEDTA did not alleviate leaf yellowing.

Height and dry weight (Figs. 1, 2) were greatest at 0.4 osmolal for the robust form and 0.8 osmolal for the dwarf form, suggesting that they may possess different salinity optima. However, the differences in height and dry weight between the forms at any given concentration were not significant. Height and dry weight did vary significantly with salinity. There were no significant interaction effects of salinity and form on height, the only character we were able to analyze by two-way ANOVA.

The maximum leaf area for the robust and dwarf forms (Table 3) occurred in the 0.4 osmolal and the 0.8 osmolal solutions, respectively, coincident with the maximum values for height and dry weight. The forms were significantly different at 0.4 osmolal ($0.01 < p < 0.05$), but not in freshwater, or in the 0.8 and 1.2 osmolal solutions. For each form, there were significant differences with salinity. Leaf area of the dwarf form was significantly greater at 0.4 and 0.8 osmolal than in freshwater or at 1.2 osmolal. Leaf area of the robust form was significantly greater at 0.4 osmolal than at 1.2 osmolal.

Differences in the leaf weight ratios between the forms was not significant (Fig. 3). This character was inversely related to salinity. Leaf weight ratio was significantly less in the 1.2 osmolal solution than in the less saline solutions.

The salinity of the root zone (5–25 cm) for Palo Alto and Alameda Creek marshes is given in Table 4. Generally, soil salinity was higher within the Alameda Creek marsh. In May, the salinity of PA 1 and 2 was significantly less than any of the three locations sampled within Alameda Creek marsh. However, the salinity of PA 3, the highest intertidal area sampled, was equal to the salinity of AC 1. Soil salinities were relatively stable throughout the Alameda Creek marsh between May and October, whereas at Palo Alto the concentration of salts of plots 2 and 3, the two higher intertidal areas, increased to levels approximately equal to those of AC 1 and 3. This type of seasonal variation is well-documented for temperate zone coastal salt marshes (Chapman 1939, 1940; Mahall and Park 1976b, Purer 1942).

Discussion

The classic approach to studying ecotypic variation within plant species is to collect specimens from populations that are phenotypically distinct under natural conditions and then grow them together under uniform conditions (Clausen et al. 1941, Goodman 1973, McMillan 1959). Any differentiation in the measured characteristics among pop-

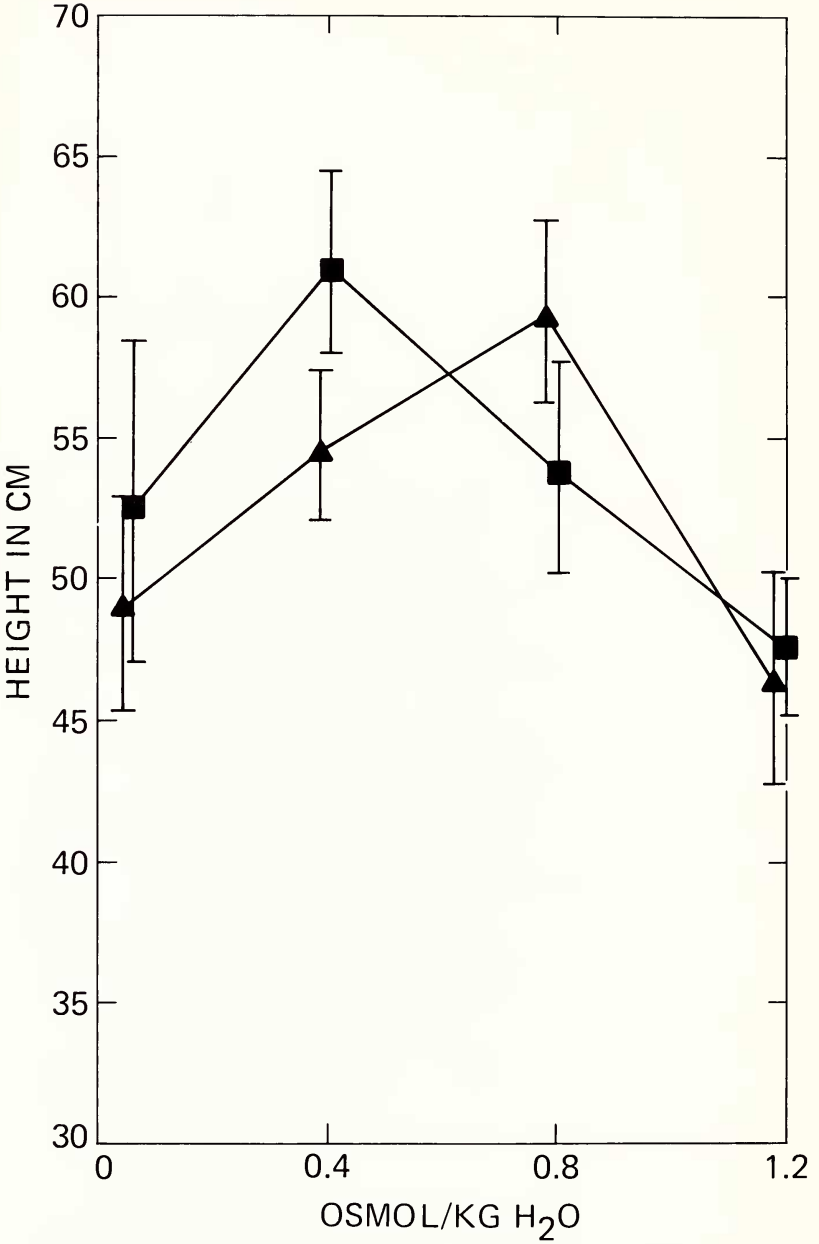

FIG. 1. Height ($\bar{Y} \pm$ S.E.) of dwarf (△) and robust (□) forms of *Spartina foliosa* grown in NaCl-treated nutrient solution.

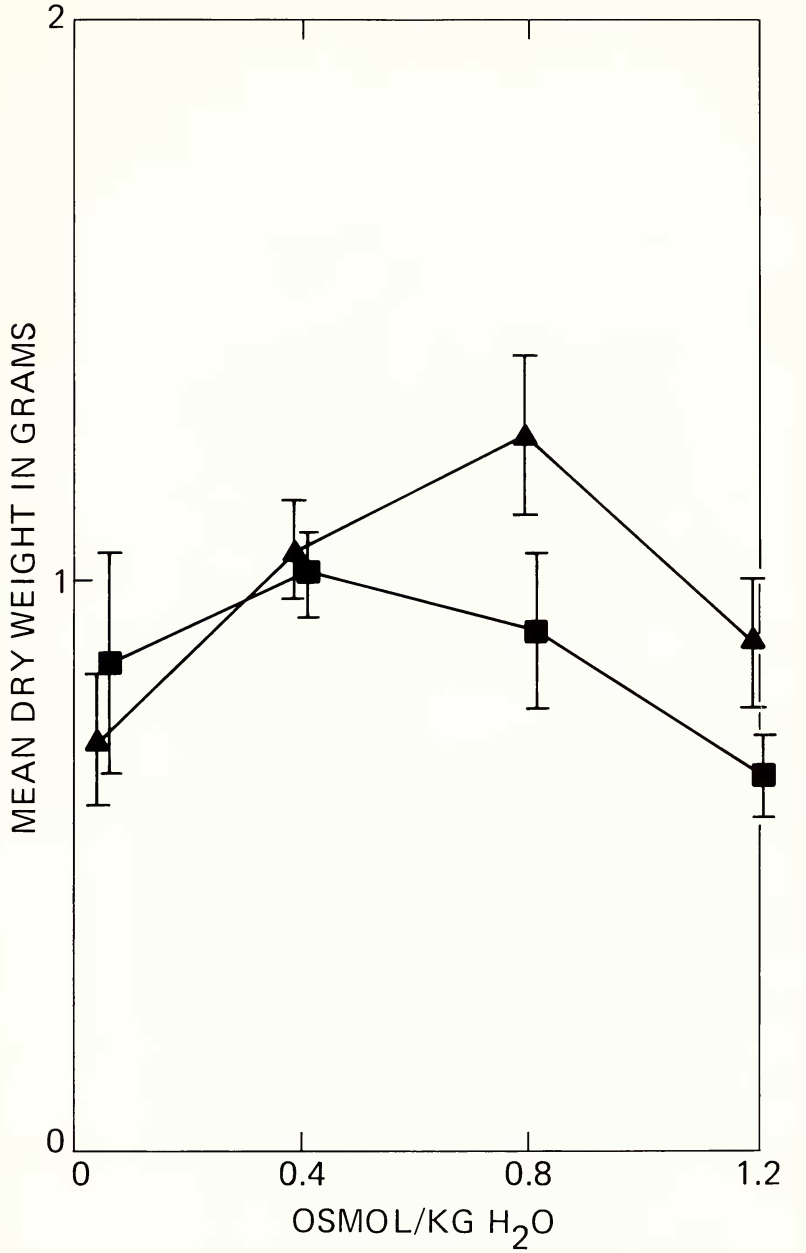

FIG. 2. Dry weight ($\bar{Y} \pm$ S.E.) of dwarf (△) and robust (□) forms of *Spartina foliosa* grown in NaCl-treated nutrient solution.

TABLE 3. MEAN LEAF AREA (CM^2 $LEAF^{-1}$) WITH 95% CONFIDENCE LIMITS OF THE DWARF AND ROBUST FORMS OF *Spartina foliosa* GROWN IN SALINE CULTURE SOLUTION.

	Dwarf	Robust
Treatment	$\bar{x}$; 95% C.L.	$\bar{x}$; 95% C.L.
0.0	7.08; 6.00–8.29	8.64; 7.13–10.2
0.4 osmolal	7.51; 6.20–8.94	10.1; 8.35–12.0
0.8 osmolal	9.49; 8.47–10.5	8.53; 7.29–9.86
1.2 osmolal	7.29; 6.00–8.76	6.76; 5.48–8.24

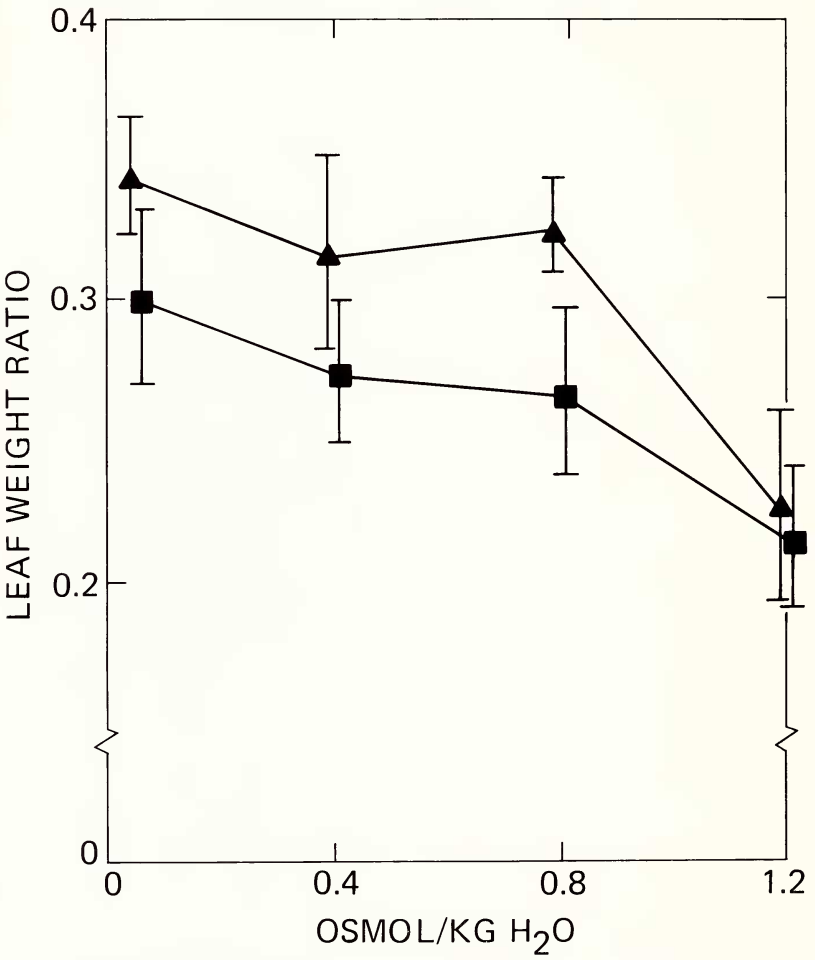

FIG. 3. Leaf weight ratio ($\bar{Y} \pm$ S.E.) of dwarf (△) and robust (□) forms of *Spartina foliosa* grown in NaCl-treated nutrient solution.

TABLE 4. SOIL SALINITY ($\bar{x} \pm$ S.E.) AS OSMOLE KG^{-1} H_2O OF ROOT ZONE OF PALO ALTO (PA) AND ALAMEDA CREEK (AC) MARSHES DURING THE 1977 GROWING SEASON. a: n = 3; n = 4 for all others.

	May			October		
	Plot			Plot		
Station	1	2	3	1	2	3
PA	0.89 ± 0.01	0.99 ± 0.01	1.05 ± 0.03	0.89 ± 0.02[a]	1.09 ± 0.04	1.18 ± 0.02
AC	1.18 ± 0.07	1.37 ± 0.02	1.30 ± 0.03	1.07 ± 0.02	1.41 ± 0.06	1.23 ± 0.02

ulations is assumed to be genetic. The results of the culturing experiment in this study indicate that the dwarf and robust forms of *S. foliosa* are not salinity ecotypes. When the experiment was started, dwarf and robust plants displayed different leaf weight ratios. However, by the end of the experiment, this distinction no longer existed. With the exception of the difference in leaf area between the forms grown at a salinity of 0.4 osmolal, dwarf and robust were not distinguishable by any of the characters measured. Furthermore, the height of dwarf *S. foliosa* grown in the laboratory exceeded the height of dwarf plants in nature, suggesting that the growth of plants at Alameda Creek is inhibited by unfavorable environmental conditions.

Significant differences in the responses of plants were associated with salinity. Survival, height, biomass and leaf area were greatest when the plants were grown under moderately saline conditions. However, in freshwater and the 0.4 osmolal solution, iron was apparently less available for plant uptake, making the direct assessment of the effect of NaCl on the growth of *S. foliosa* in those solutions difficult. Iron chlorosis was not severe in the two highest NaCl concentrations, indicating that iron was more available and not limiting plant growth. Inhibition of plant growth occurred over a narrow range of salinity between 0.8 and 1.2 osmolal. This inhibition was probably due to energy expended maintaining the internal salt balance, a process regulated by actively secreting salts through salt glands. Mahall and Park (1976b) found that shoot growth of cultured *S. foliosa* was significantly reduced at concentrations greater than 0.6 osmole kg^{-1} H_2O. The reduction in leaf weight ratio with increasing salinity may be an aspect of a common strategy in the adjustment of a plant to salinity by which the transpirational surface area is decreased relative to the water absorbing surface area (Bernstein and Hayward 1958).

Because soil salinities were recorded at the beginning and end of the growing season, we have no detailed information on how long plants from the two marshes and from different intertidal areas of the same marsh were exposed to particular salinities. These data would be valuable if growth rate is an integrated response to salt concentra-

tion over time. Assuming that it is, and using the available data, soil salinity at Alameda Creek appeared to remain relatively high throughout the growing season, suggesting that plant growth may be inhibited by prolonged salinity stress. At Palo Alto, soil salinity increased with increasing distance from the shoreward edge of the marsh, and, unlike Alameda Creek, displayed a seasonal increase that was increasingly more pronounced at higher intertidal areas. Salinity of the lowest intertidal area, PA 1, was seasonally constant, but at PA 2 salinity increased in October to concentrations equal to those recorded at Alameda Creek. However, the duration of exposure to the October concentrations may have been relatively brief. Plants at PA 3 (where height and biomass were reduced relative to plants at PA 1 and PA 2) were continuously exposed to concentrations as high as those recorded at Alameda Creek. Thus soil salinity conditions, at least in terms of concentration and duration of exposure, were similar between PA 3 and Alameda Creek, the two areas where dwarf plants occur.

In this study, only one environmental factor, salinity, was examined. It is rather unlikely that single cause and effect relationships affecting variation are prevalent in nature (Gould and Johnston 1972). Also, the occurrence of polygenic inheritance systems (Nobs and Hiesey 1957) indicates that the physiological and morphological response of an individual may depend upon the interaction of several environmental components within the genotype. Therefore, it cannot be discounted that the dwarf and robust forms would not segregate under a different set of factors. Nonetheless, the salinity effects observed for cultured plants complement the findings of the field survey: dwarf plants were associated with soils that displayed relatively high soil salinity throughout the growing season, whereas robust plants occurred in less saline soils. The results of this study, consistent with those of Harvey (1976) for *S. foliosa* and Mooring et al. (1971) and Nestler (1977) for *S. alterniflora,* indicate that the height forms of *S. foliosa* are ecophenes, and that the phenotypic expression of the species is partially a function of soil salinity.

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